

PRELIMINARY INSIGHTS INTO THE PHYLOGENY AND SPECIATION OF *SCALESIA* (ASTERACEAE), GALÁPAGOS ISLANDS

Jeremy D. Blaschke

Bryan College # 7071
721 Bryan Dr.
Dayton, Tennessee 37321, U.S.A.
jblaschke0998@bryan.edu

Roger W. Sanders

Bryan College # 7802
721 Bryan Dr.
Dayton, Tennessee 37321, U.S.A.
rsanders@bryan.edu

ABSTRACT

Scalesia Arn. (Asteraceae: Heliantheae) is a woody genus of fifteen species endemic to the Galápagos Islands. Morphological, distribution, and habitat data pertinent to speciation patterns in *Scalesia* were extracted from the literature and selected auxiliary specimens. All species of *Scalesia*, *Pappobolus* S.F. Blake, and *Simsia* Pers., along with selected species of *Viguiera* Kunth, were subjected to phylogenetic analysis (63 characters in 78 taxa). Homoplasy and incongruence among resulting trees prevented resolution of relationship and comparison of speciation events relative to its sister-group. Morphologically, species throughout these genera are marked primarily by homoplastic apomorphies. Based on broad characterization of habitats, morphological divergence (except for arborescence) and habitats appear to be poorly correlated. Sampling for future studies should be extended to include other groups in the derived Helianthinae.

RESUMEN

Scalesia Arn. (Asteraceae: Heliantheae) es un género leñoso de quince especies, endémico de las Islas Galápagos. Los datos morfológicos, de distribución y de hábitat relativos a los patrones de especiación en *Scalesia* se obtuvieron de la bibliografía y de especímenes auxiliares seleccionados. Todas las especies de *Scalesia*, *Pappobolus* S.F. Blake, y *Simsia* Pers., junto con algunas especies de *Viguiera* Kunth, fueron objeto de un análisis filogenético (63 caracteres en 78 taxa). La homoplasia e incongruencia entre los árboles resultantes impidió la resolución de parentesco y comparación de eventos de especiación relativa a su grupo hermano. Morfológicamente, las especies de estos géneros se distinguen primariamente por apomorfías homoplásticas. Basados en la amplia caracterización de los hábitats, la divergencia morfológica (excepto la arborescencia) y los hábitats parecen estar pobremente correlacionadas. El muestreo para futuros estudios debe ampliarse para incluir otros grupos de Helianthinae derivadas.

INTRODUCTION

Scalesia Arn. (Asteraceae: Heliantheae: Helianthinae) comprises fifteen species, all endemic to the Galápagos Islands. Howell (1941) accepted 18 species in four sections and related it to the Ecliptinae Lessing. Based on extensive field study, Eliasson (1974) recognized only 14 species, avoided the use of sections, discussed aspects of character evolution, and placed the genus in the Helianthinae Dumort. Hamann and Wium-Andersen (1986) described an additional species.

Recent studies on *Scalesia* have focused on intergeneric relationships (Schilling et al. 1994; Spring et al. 1999; Panero 2007), chemical diversity (Adersen & Baerheim Svendsen 1986; Spring et al. 1997, 1999; Petersen et al. unpubl.), anatomy (Carlquist 1982), autecology (Itow 1995; Kitayama & Itow 1999; Hamann 2001), adaptive reproductive strategies (McMullen & Naranjo 1994; Nielsen et al. 2002, 2007), and population structure (Nielsen et al. 2003; Nielsen 2004). Chloroplast DNA restriction site analysis suggests that *Scalesia* belongs to a group of specialized genera, the “derived Helianthinae,” that are embedded within a derived clade of *Viguiera* Kunth (Schilling et al. 1994). *Viguiera*, whose taxonomy has been unresolvable on morphological grounds, appears as a paraphyletic assemblage basal to all other genera in the Helianthinae on the basis of cpDNA restriction sites and internal transcribed spacer (ITS) sequences of nuclear ribosomal DNA (Schilling & Jansen 1989; Schilling & Panero 2002). In an analysis in which *S. pedunculata* Hook.f. and several species of *Pappobolus* S.F. Blake were sampled (Schilling et al. 1994), *Scalesia* and *Pappobolus* were sister groups, and the next closest clade consisted of *Simsia* Pers. plus *Viguiera* ser. *Pinnatilobatae* S.F. Blake. However, the authors noted problems with interpretation of the three restriction sites synapomorphic for *Scalesia* and *Pappobolus* and concluded, “Thus, the relative relationships among *Scalesia*, *Pappobolus*, *Simsia*

and *Viguiera* ser. *Pinnatilobatae* are not well resolved by these data.” Indeed, subsequent work has shown that chloroplast restriction sites, chloroplast genes, and ITS regions lack sufficient variation to resolve relationships in the derived *Helianthinae* (Schilling & Panero 1996, 2002; Petersen et al. unpubl.). However, recent analyses using external transcribed spacer (ETS) regions did find sufficient diversity to resolve species of *Helianthus* (Timme et al. 2007), a member of the derived *Helianthinae*, as well as species in other genera of the *Heliantheae*, such as *Montanoa* (Plovanich & Panero 2004).

Our interest is primarily in patterns of diversification, homoplasy, speciation rates, and degree of adaptation using *Scalesia* because it is the most speciose endemic angiosperm genus in the Galápagos. It is of interest that homoplasy among morphological characters of *Simsia* species prevented Spooner (1990) from publishing a cladistic analysis in his monograph. Likewise, Panero (1992) chose not to include phylogeny in his monograph of *Pappobolus*, instead recognizing only phenetic groupings. Thus, notable amounts of unanalyzed data are available in the literature for addressing the issue of homoplasy across *Scalesia* and relations. While it is our hope in the future to sample ETS regions in *Scalesia* species to determine their applicability in phylogenetic analysis, as well as use molecular phylogenies in investigating issues of interest to us, our goal here is to mine the existing pertinent morphological and ecological data that are available in the literature to provide a comparative context for later molecular studies. That is, we seek to provide insights into: **1)** sister-group and intrageneric relationships of *Scalesia*, **2)** homoplastic traits, **3)** relative amounts of speciation per clade, and **4)** directions for future molecular sampling. We anticipate that phylogenetic analysis of morphology may not yield consistent assessments of relationships or be congruent with molecular phylogenies (for example, see Plovanich and Panero [2004] concerning homoplasy in morphological taxonomic criteria in the *Heliantheae*). However, that result is not certain, for the hand-calculated Wagner parsimony networks of morphological data of *Dendroseris* and *Robinsonia* (Sanders et al. 1987), two other island endemics of the *Asteraceae* (*Lactuceae* and *Senecioneae*, respectively), did prove to be congruent with later molecular phylogenies (Crawford et al. 1992; Sang et al. 1995).

METHODS

Data.—Taxon sampling is based on the sister-group conclusions and Figure 1 of Schilling et al. (1994) and availability of supplemental specimens at the Botanical Research Institute of Texas and Bryan College. Morphological traits, coded as binary and multistate unordered characters, were extracted from published monographs of *Pappobolus* (Panero 1992), *Scalesia* (Eliasson 1974; Hamann & Wium-Andersen 1986), *Simsia* (Spooner 1990), and species representing *Helianthus* L. (Schilling 2006), *Viguiera* sect. *Maculatae* (S.F. Blake) Panero & Schilling (Panero & Schilling 1988), and the outgroup *Bahiopsis* Kellogg (Schilling 1990). Selected dried specimens were consulted to verify codings obtained from the literature, supply missing data, and score representative species from *Viguiera* ser. *Grammatoglossae* S.F. Blake and ser. *Pinnatilobatae* (Table 1). Characters were chosen to maximize distinctions within *Scalesia*, *Pappobolus*, and *Simsia* and scored accordingly in the remaining taxa (Table 2), resulting in a number of characters being coded as polymorphisms. The compiled data constitute 63 characters in 78 species (Appendix).

Phylogenetic Analysis.—Parsimony analysis was conducted using PAUP* 4.0b10 (Swofford 1998). Heuristic searches were made with character optimization set to both accelerated and delayed transformation and with the following options: character weighting equal, 10 rounds of random addition sequence with 100 trees held at each addition, branch swapping by tree-bisection, MulTrees in effect, MaxTrees=100,000. Bootstrap analysis (10,000 replicates) was conducted using accelerated transformation by heuristic search with 10 trees held at each addition step. A final heuristic search, in which the majority-rule consensus tree from the bootstrap analysis was input for branch swapping only, was conducted using accelerated transformation with options as above. Based on the strict consensus tree from the first heuristic search, a reduced matrix of only the ancestral nodes of the outgroup, *Helianthus*, *Pappobolus*, *Simsia*, and *Viguiera* *grammatoglossa* + *V. stenophylla*; the remaining *Viguiera* species; and the species of *Scalesia* was generated. This matrix was subjected to a branch-and-bound search (options: accelerated transformation, equal weighting, MulTrees in effect, furthest addition sequence) and bootstrap analysis as above.

TABLE 1. Herbarium specimens consulted to supplement and verify data in literature. BRYAN is not yet officially recognized by Index Herbariorum but is used provisionally to designate the Henning Natural History Museum of Bryan College.

Taxon	Specimen	Locality	Herbarium
Bahiopsis			
<i>B. deltoidea</i> A. Gray	<i>S. White</i> 5042	Mexico: Baja, California. La Paz	SMU
<i>B. parishii</i> Greene	<i>Mahler & Thieret</i> 5440	USA: Arizona: Maricopa Co.: Sagauero Lake	SMU
Helianthus			
<i>H. annuus</i> L.	<i>W. L. Henning</i> Acc. No. B 802	USA: Missouri: Boone Co.: W of Columbia	BRYAN
	<i>G. Varga</i> Acc. No. B 1794	USA: Tennessee: Rhea Co.	BRYAN
<i>H. tuberosus</i> L.	<i>W. L. Henning</i> Acc. No. B 804	USA: Missouri: Boone Co.: S of Columbia	BRYAN
Pappobolus			
<i>P. acutifolius</i> (S.F. Blake) Panero	<i>Panero & Galán</i> 1399	Perú: Ancash: Caráz	BRIT
<i>P. matthewsii</i> (Hochr.) Panero	<i>J. Panero</i> 1353	Perú: Amazonas: Pedro Ruiz	BRIT
<i>P. robinsonii</i> Panero	<i>Panero & Sánchez</i> 1225	Perú: Cajamarca: Celendin	BRIT
<i>P. steubelii</i> (Hieron.) Panero	<i>Panero et al.</i> 932	Perú: Cajamarca: Chalhuyayaco	BRIT
Scalesia			
<i>S. affinis</i> Hook.f.	<i>Mears</i> 5296	Ecuador: Galápagos: Floreana	BRIT
<i>S. helleri</i> B.L. Rob.	<i>Mears</i> 5494	Ecuador: Galápagos: Santa Fe	BRIT
<i>S. stewartii</i> L. Riley	<i>Mears</i> 5556	Ecuador: Galápagos: Bartolomé	BRIT
<i>S. villosa</i> A. Stewart	<i>Mears</i> 5226	Ecuador: Galápagos: Gardner	BRIT
Simsia			
<i>S. amplexicaulis</i> (Cav.) Pers.	<i>A. Cronquist</i> 9611	Mexico: Michoacán: La Piedad	SMU
<i>S. calva</i> A. Gray	<i>J. Rodriguez</i> 64	Mexico: Nuevo León: Vallecillo	SMU
	<i>U. Waterfall</i> 16660	Mexico: Coahuila: Sabinas	SMU
<i>S. eurylepsis</i> S.F. Blake	<i>U. Waterfall</i> 14300	Mexico: San Luis Potosí: Ciudad de Valles	SMU
<i>S. foetida</i> (Cav.) S.F. Blake	<i>Yen & Estrada</i> 6479	Mexico: Chihuahua: Presa Chihuahua	BRIT
<i>S. fruticulosa</i> (Spreng.) S.F. Blake	<i>King & Guevara</i> 5817	Colombia: Cundinamarca. Chipaque	SMU
<i>S. holwayi</i> S.F. Blake	<i>R. M. King</i> 7337a	Guatemala: Alta Verapaz: San Cristóbal Verapaz	BRIT
<i>S. sanguinea</i> A. Gray	<i>C. G. Pringle</i> 11513	Mexico: Jalisco: Guadalajara	SMU
Viguiera ser. Grammatoglossae			
<i>V. cordifolia</i> A. Gray	<i>J. Cornelius</i> 227	USA: Texas: Brewster Co.: Black Gap WMA	SMU
	<i>D. S. Correll</i> 15006	USA: Texas: Jeff Davis Co.: Davis Mts.	SMU
<i>V. grammatoglossa</i> DC.	<i>J. Rzedowski</i> 34497	Mexico: Oaxaca. Chilapa de Díaz	VDB
Viguiera sect. Maculatae			
<i>V. adenophylla</i> S.F. Blake	<i>E. Estrada</i> 1889	Mexico: Nuevo León. Iturbide	BRIT
Viguiera ser. Pinnatilobatae			
<i>V. stenoloba</i> S.F. Blake	<i>A. Krings</i> 288	USA: Texas: Presidio Co.: Big Bend Ranch State Park	BRIT
	<i>Nee & Diggs</i> 25354	Mexico: Edo. Coahuila. Mun. San Pedro	BRIT
	<i>A. Treverse</i> 2215	USA: Texas: Brewster Co.: Big Bend National Park	BRIT

Bayesian analysis was conducted using MrBayes v3.1.2 (Huelsenbeck & Ronquist 2001) on both the full and the reduced matrices using the default settings of the standard discrete evolutionary model. Analysis of the full matrix was run for 200,000,000 generations and sampled once every 100,000 generations; the reduced matrix was run for 400,000 generations and sampled every 100 generations.

Habitat Characterization.—Geographic distributions and habitat features were estimated from Cronquist (1971), Eliasson (1976), Hamann and Wium-Andersen (1986), and personal observation of one of us (RWS).

TABLE 2. Characters and character states used in data matrix (Appendix). Character states are unordered.

1. Habit 0: shrub, 1: tree, 2: suffrutescent perennial, 3: perennial herb, 4: annual	31. Phyllary pubescence density 0: revealing surface, 1: obscuring surface
2. Hair type presence 0: unspecialized pubescent, 1: villous to lanate, 2: scabrous or strigose	32. Phyllary margin, cilia 0: without cilia, 1: ciliate
3. Glandular trichomes 0: absent, 1: present	33. Phyllary tip shape 0: blunt or abruptly acute, 1: acuminate, long acute
4. Twig pubescence color 0: white to gray, 1: yellow or green	34. Phyllary tip orientation 0: erect or appressed, 1: reflexed or spreading
5. Leaf phyllotaxy 0: alternate, 1: opposite	35. Phyllary base thickness 0: unthickened, herbaceous, 1: base slightly thickened indurate, 2: base conspicuously thickened indurate
6. Leaf heterochrony 0: inflorescence leaves \pm size of cauline lvs., 1: lvs. partially or gradually reducing into inflor., 2: lvs. much reducing into inflor.	36. Ray presence 0: absent, 1: present in full complement, 2: present in part
7. Leaf outline 0: ovate, 1: lanceolate, 2: cordate, 3: triangular, 4: elliptic, 5: linear-oblong	37. Ray orientation 0: spreading, 1: strongly reflexed or recurved
8. Leaf margin lobing 0: unlobed, 1: lobed 1/4 to midrib, 2: lobed 1/2 to midrib, 3: lobed 3/4 to midrib, 4: regularly deeply lobed nearly to midrib	38. Ray ligule length 0: <1.5 cm, 1: 1.5–3.0 cm, 2: > 3 cm
9. Leaf margin serration 0: completely entire, 1: crenate or serrulate, indistinctly toothed, 2: distinctly serrate	39. Ray apex fusion 0: shallowly 2-3 toothed, 1: deeply 2-3 notched/lobed, 2: irregularly, barely fused or lipped
10. Leaf margin orientation 0: flat, 1: revolute	40. Ray ovary shape 0: ovoid/lenticular/fusiform, 1: linear
11. Leaf adaxially strigose 0: not strigose, scabrous, or sericeous, 1: moderately strigose, scabrous, or sericeous, 2: densely strigose, scabrous, or sericeous	41. Palea length 0: about equalling phyllaries, 1: protruding above phyllaries, 2: shorter than phyllaries
12. Leaf abaxially strigose 0: not strigose, scabrous, or sericeous, 1: moderately strigose, scabrous, or sericeous, 2: densely strigose, scabrous, or sericeous	42. Palea apex pubescence 0: glabrous, 1: pubescent
13. Leaf abaxially lanate 0: not villous or lanate, 1: moderately villous or lanate, 2: densely villous or lanate	43. Palea segmentation 0: lacking, 1: shallow, 2: deep
14. Leaf surface reflectance, adaxially 0: dull, 1: shiny	44. Palea segments, shape 0: elliptic, 1: triangular, 2: ovate-rounded, 3: subulate, 4: oblong-ligulate
15. Leaf texture 0: herbaceous/chartaceous, 1: leathery, 2: thinly membranous	45. Palea segments, orientation 0: erect, 1: diverging or reflexed, 2: strongly overlapping, 3: inflexed or hooded
16. Leaf venation 0: triplinerved, 1: pinninerved	46. Palea segments, central one 0: equal to laterals, 1: much longer than laterals
17. Leaf midrib position adaxially 0: level or above surface, 1: sunken below surface	47. Disk corolla color 0: yellow to orange, 1: brown, 2: pale yellow, 3: white, 4: pink, 5: deep purple
18. Petiole shape 0: unwinged, 1: wing tapering in apex, 2: wing tapering above base, 3: wing broad to basal insertion, 4: winged at base only	48. Disk corolla tube to throat length ratio 0: ~3–4, 1: ~5–10, 2: ~1
19. Petiole length 0: 0–9 mm, 1: >10 mm	49. Disk corolla tube pubescence 0: glabrous, 1: puberulent
20. Inflorescence reiteration 0: monochasial, 1: dichasial	50. Disk corolla throat pubescence 0: glabrous, 1: puberulent
21. Head arrangement 0: more/less solitary, 1: open panicle, 2: tightly aggregate panicle	51. Disk corolla lobes abaxially 0: without dark pigment, 1: with black pigment, 2: with purple pigment
22. Head size (w/o rays) 0: very large >30 mm, 1: large 15–30 mm, 2: moderate 7–15 mm, 3: small <7 mm	52. Anther color 0: yellow, 1: black, 2: (yellow) purple distally, 3: maroon or brown
23. Involucre shape 0: campanulate-subcylindric, 1: urceolate-hemispheric	53. Anther appendix color 0: stramineous, 1: all or part black, 2: white
24. Phyllary series 0: 3–4, 1: 2, 2: (4–)5–6	54. Style branch color abaxially 0: without black pigment, 1: with black pigment
25. Phyllary shape 0: oblong to obtrullate, 1: narrowly elliptic, 2: lanceolate, 3: subulate-attenuate, 4: ovate	55. Style branch apex 0: deltate, 1: attenuate
26. Phyllary, outer series, shape 0: not spatulate, 1: spatulate	56. Style branch appendage 0: absent, 1: present
27. Phyllary size to florets 0: subtending florets, 1: overtopping florets	57. Achene length 0: < 3 mm, 1: 3–5 mm, 2: > 5 mm
28. Phyllary size ratio, outer/inner 0: outer \pm inner, 1: outer < 2/3 inner	58. Achene pubescence 0: glabrous, 1: sericeous
29. Phyllary color 0: normal green, 1: stramineous \pm with green stripes, 2: blackish green, 3: purple	59. Achene compression 0: biconvex-lenticular, 1: laterally flat but slightly biconvex, 2: strongly lat. flattened, 3: terete or trigonous
30. Phyllary consistency 0: scale-like, 1: foliaceous	60. Pappus development 0: absent, 1: callous ring only, 2: awns and/or scales
	61. Pappus, no. awns 0: 0, 1: 1 (often small), 2: 2, 3: multiple
	62. Pappus, intervening scales 0: absent, 1: present
	63. Pappus persistence 0: persistent, 1: caducous

RESULTS

Sister-group relationships.—The first two heuristic searches (random-addition with accelerated vs. delayed character transformations) resulted in 100,000 shortest trees each (442 steps). These and their strict consensus trees were partially incongruent with the majority-rule tree of the bootstrap analysis. In the delayed transformation search, *Viguiera adenophylla* was sister to all other ingroup taxa, and *Pappobolus* was paraphyletic with *P. ecuadoriensis* sister to all remaining taxa. Of these, one clade contained *P. sagasteguii*, a subclade of *V. stenoloba* + *Scalesia*, and a subclade containing the remaining *Viguiera* species, *Helianthus*, and *Simsia* as monophyletic genera. The other clade contained all remaining species of *Pappobolus*. The accelerated transformation search resulted in *V. adenophylla* as above but the remaining ingroup taxa constituted five clades in an unresolved polytomy: *V. cordifolia*, *Helianthus*, *Scalesia*, *Simsia*, and one having a monophyletic *Pappobolus* sister to *V. grammatoglossa* + *V. stenoloba*.

The third heuristic search (bootstrap majority-rule tree input and branches swapped) resulted in all 100,000 trees being congruent with the bootstrap analysis, though one step longer (443) than the trees from the first two searches. In the strict consensus tree of this analysis (Fig. 1), the ingroup formed three major clades. A monophyletic *Pappobolus* was sister to the remaining ingroup taxa. Of these, one clade consisted of *V. adenophylla* and *Scalesia* as sister groups. The other clade contained a tetrachotomy: *Simsia*, *Helianthus*, *V. cordifolia*, and *V. grammatoglossa* + *V. stenoloba*.

The Bayesian majority-rule consensus tree (analysis final average standard deviation 0.0078) added yet another possible arrangement. Of the ingroup taxa, *Scalesia* + *V. adenophylla* were sister to the remainder, which formed a polytomy: *V. grammatoglossa*, *V. stenoloba*, nine species of *Pappobolus*, a clade with all the remaining *Pappobolus*, and a clade consisting of *V. cordifolia*, *Helianthus*, and *Simsia*.

In all of the consensus trees, *Simsia* was completely unresolved or nearly so, and *Pappobolus* contained two to three large sets of unresolved species. *Scalesia* was reasonably well resolved but its topology differed among trees. All heuristic searches found the arboreous species as a resolved clade (*S. cordata* A. Stewart, *S. microcephala* B.L. Rob., *S. pedunculata* basal), the lobe-leaved species (*S. baurii* Robinson & Greenman, *S. helleri* Robinson, *S. incisa* Hook.f., *S. retroflexa* Hemsl.) as a partially or fully resolved clade, the three species with elongate phyllaries (*S. atractylodes* Arn., *S. stewartii* L. Riley, *S. villosa* A. Stewart basal) as a grade or clade, and a clade of *S. divisa* Andersson + *S. gordilloi* O.J. Hamann & Wium-And. In two searches the arboreous clade was sister to the remainder with the elongate-bracted clade deeply imbedded; in the third the elongate-bracted group was a basal grade with the arboreous clade deeply imbedded. In the Bayesian majority rule tree, *Scalesia* was an eight-way polytomy of the arboreous, elongate-bracted, and lobe-leaved clades, *S. affinis* Hook.f., *S. aspera* Andersson, *S. crockeri* J.T. Howell, *S. divisa*, and *S. gordilloi*.

Branch-and-bound analysis of the reduced matrix produced 13 trees of equal length (163 steps). In the strict consensus tree (Fig. 2), *V. adenophylla* was sister to the other ingroup taxa, which formed a tetrachotomy: *Scalesia*, *Helianthus*, *Simsia* + *V. cordifolia*, and *Pappobolus* + the *V. grammatoglossa-stenophylla* ancestor. In *Scalesia*, the arboreous clade (unresolved) was sister to the remainder which formed a polytomy of *S. affinis*, *S. aspera*, *S. crockeri*, *S. divisa*, *S. gordilloi*, a partially resolved clade of the lobe-leaved species, and a resolved elongate-bracted clade. However, the Bayesian majority rule tree (analysis final average standard deviation 0.0070) of the reduced matrix differed by being nearly identical to one of the most parsimonious branch-and-bound trees (Fig. 2) except that 1) the arboreous species formed a basal grade with *S. cordata* + *S. microcephala* sister to the remaining species, 2) there was no resolution among *S. affinis*, *S. aspera*, *S. crockeri* and the remaining clades, and 3) *S. retroflexa* was basal to the other members of the lobe-leaved clade.

Apomorphies and homoplasy.—In one of the 100,000 equally parsimonious trees from the third heuristic search the composite consistency index (CI) was 0.24 (excluding two uninformative characters), the rescaled CI (RC) was 0.17, and the retention index (RI) was 0.71. In this tree, the only synapomorphies of *Scalesia* with a consistency index over 0.4 were ray florets absent and anthers black. The only comparable synapomorphy for *Pappobolus* was anthers yellow and for *Simsia*, phyllaries not thickened at base and achenes strongly laterally flattened.

The composite CI of the branch-and-bound trees (Fig. 2) was 0.49 (including only 51 informative char-

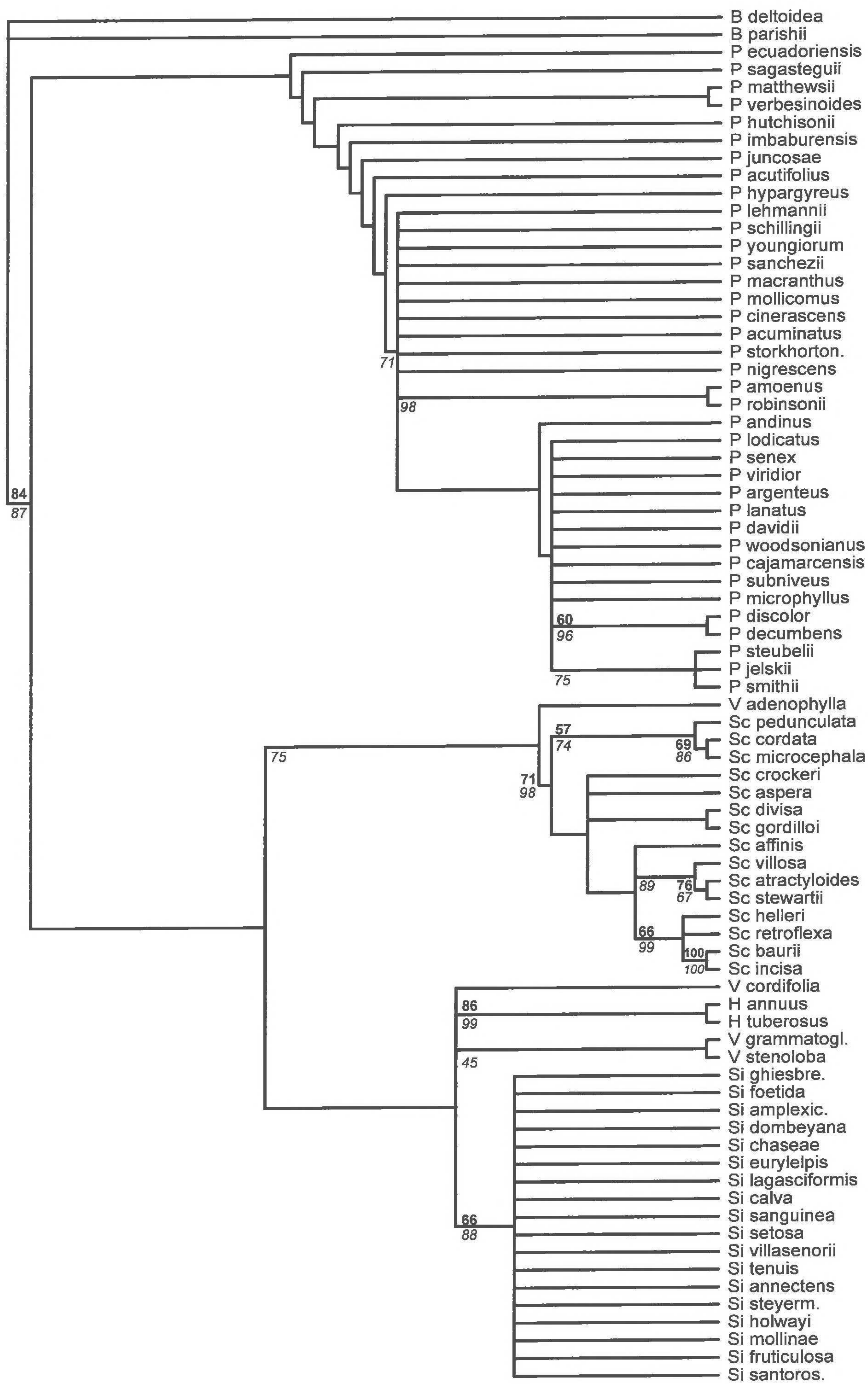


FIG. 1. Strict consensus tree of third heuristic search (branch-swapping of input bootstrap majority-rule tree) of full data matrix, based on 100,000 equally parsimonious trees. Bold numbers above branches indicate bootstrap values; italic numbers below branches indicate Bayesian posterior probabilities. Generic abbreviations: B=*Bahioopsis*, H=*Helianthus*, P=*Pappobolus*, Sc=*Scalesia*, Si=*Simsia*, V=*Viguiera*.

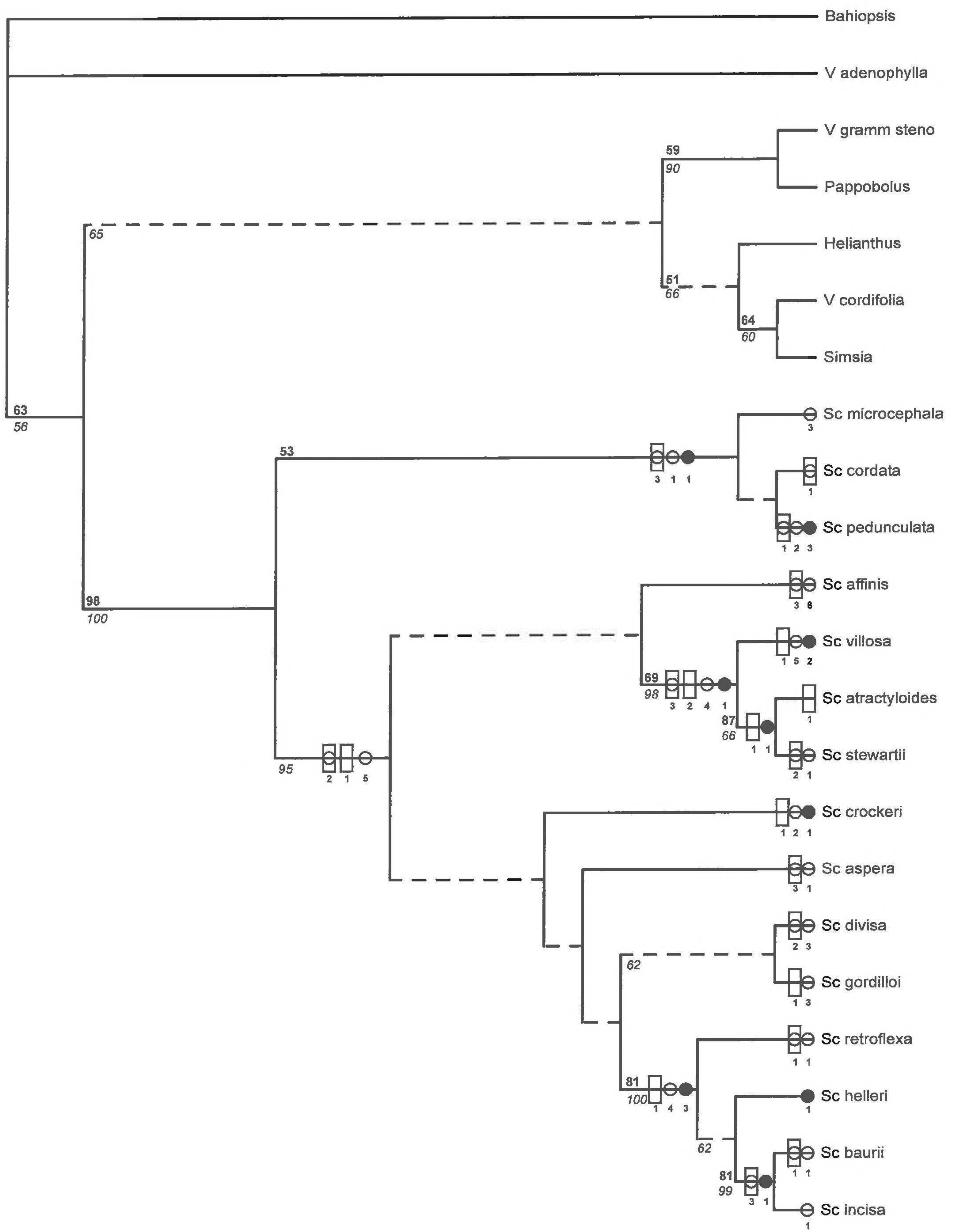


FIG. 2. One of 13 equally parsimonious trees obtained from branch-and-bound analysis of *Scalesia*. Bold numbers above branches indicate bootstrap values; italic numbers below branches indicate Bayesian posterior probabilities. Dashed lines indicate branches that are collapsed in the resulting strict consensus tree. Generic abbreviations are as in Figure 1. Numbers of apomorphies on branches of *Scalesia* by class as follows: solid dot = unique (synapomorphies/autapomorphies), open circles = homoplasy restricted to species of *Scalesia*, box = homoplasy between *Scalesia* and another genus, box with circle = homoplasy both within *Scalesia* and with external genus.

acters), the RI 0.66, and RC 0.37. In this tree, the synapomorphies for *Scalesia* supported by a consistency index of 0.4 or greater included: capitula 15-30 cm diameter; involucre hemispheric to urceolate; phyllaries oblong to obtrullate and erect/appressed; ray absent but, when present deeper within the clade, reflexed with irregularly fused lobes; paleae deeply segmented; corollas white; anther appendices white; and achenes glabrous. Black anthers, instead, appeared to be synapomorphic for the ingroup minus *V. adenophylla*.

The third heuristic search of the full matrix resulted in only six characters that were completely consistent: four involved autapomorphies (or synapomorphies for species pairs), whereas only three involved synapomorphies of significant clades. Eleven homoplastic characters had consistency indices of 0.5 or higher. Four of these (phyllary base thickening, ray presence, fusion of ray lobes, and shape of palea segments) were parallelisms or reversals within *Scalesia*; only two (growth habit, orientation of palea segments) were parallelisms between species of *Scalesia* and other genera. Forty-six characters had consistency indices lower than 0.5, of which 30 appeared in both *Scalesia* and other genera, 15 in only other genera, and only one (ratio of corolla tube to limb lengths) just in *Scalesia*.

The branch-and-bound matrix had only 55 variant characters. Sixteen were consistent, and, of these, eleven involved synapomorphies of significant clades. Twenty-five characters were homoplastic with a consistency index of 0.5 or higher including nine appearing within *Scalesia* and six in *Scalesia* and related genera. Only 14 characters were below the 0.5 consistency index level with only one restricted to species of *Scalesia* (as above), only one outside of *Scalesia*, and the remaining 12 appearing in both *Scalesia* and other genera.

Geographic distributions and ecology.—All species except *Scalesia affinis*, which is sympatric with *S. aspera*, *S. crockeri*, *S. helleri*, *S. retroflexa*, and *S. villosa*, are narrowly allopatric or parapatric (Fig. 3). Some have disjunct populations occurring on separate islands. All the arboreous species (*S. pedunculata*, *S. cordata*, and *S. microcephala*) are found in the moist forest zone in mid to upper elevation and are geographically isolated from each other. *Scalesia affinis*, the only species with consistently radiate capitula, has the widest distribution and occupies the widest range of habitats; occurring most commonly in the arid zone, it ranges from coastal to lower parts of the moist forest zone. All remaining species are found in the low elevation (littoral, arid, and dry forest zones) (Table 2). Due to overlap of preferences, there appears to be little habitat differentiation among these species. Only the rare species *S. crockeri* and *S. retroflexa* are known only from littoral sites. Other species (e.g., *S. atractyloides*; Mauchamp et al. 1998) are restricted to cliffs due to grazing by feral goats but historically ranged over more littoral and arid sites.

DISCUSSION

Phylogenetic relationships.—The present results support the monophyly of *Scalesia*, *Simsia*, and *Helianthus*. Although molecular data (Schilling et al. 1994) support *Pappobolus* as monophyletic, the present data are equivocal in that regard, in some cases placing *Scalesia*, *Simsia*, *Helianthus*, and associated *Viguiera* species within a paraphyletic *Pappobolus*.

Morphological data do not resolve the sister-group relationships of *Scalesia*, leaving open the possibility that *Scalesia* is sister to a group of *Viguiera* species or that *Scalesia* arose more or less simultaneously with *Simsia*, *Helianthus*, and *Pappobolus* (with any associated *Viguiera* species). As *Viguiera* sect. *Maculatae* is basal among the derived Helianthinae based on DNA restriction site and ITS data (Schilling & Jansen 1989; Schilling et al. 1994; Schilling & Panero, 1994, 1996, 2002), the sister-group placement of *Scalesia* and *V. adenophylla* in some results is due possibly to experimental error in coding or identification. Furthermore, Schilling and Panero's (1996) molecular analysis suggests that *Tithonia* Desf. ex Gmelin, *Viguiera* subg. *Amphilepis* S.F.Blake, and *V.* sect. *Paradosa* S.F.Blake are closer to *Pappobolus* than is *Simsia* and should be considered as potential sister groups of *Scalesia*.

Within *Scalesia* there is general support for the lobe-leaved, arboreous, elongate-bracted, and *divisagordilloi* clades. Because the arboreous clade did not receive support from a minority of analyses, it is interesting that Eliasson (1974) considered *S. pedunculata* to have developed arborescence convergently with *S. cordata* and *S. microcephala*. If all variant trees based on the various analyses performed are considered, the only clades receiving total support are the lobe-leaved clade and a terminal clade of *S. atractyloides* and *S.*

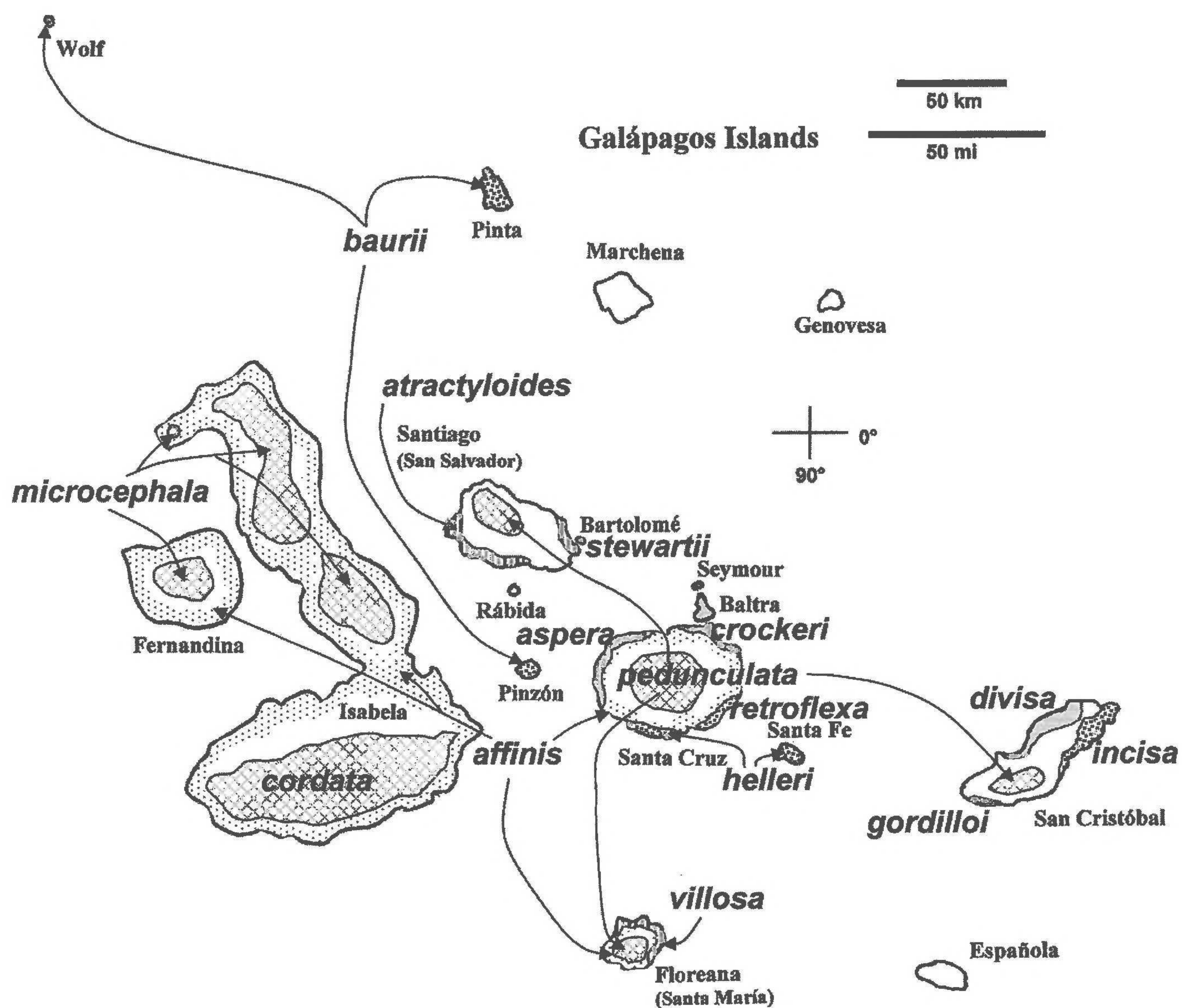


FIG. 3. Distribution of *Scalesia* species, estimated from literature, including historically known ranges. Fine stippling = *Scalesia affinis*, course stippling = lobe-leaved clade; cross hatching = arboreous clade, vertical lines = elongate-bracted clade, solid dark gray = *divisa-gordilloi* clade; solid light gray = remaining species.

stewartii, more in line with Eliasson's conclusions. Within the lobe-leaved clade, there is total support for *S. baurii* and *S. incisa* as a clade, but only partial support for *S. helleri* + *S. retroflexa*. In this case, these clades and all remaining species would radiate from a basal polytomy. If, indeed, *Scalesia* is an example of radiation by the rapid dispersal of founder populations from an initial colonizer, an unresolved basal polytomy may portray more accurately the history of *Scalesia* than any of the less-supported but more-resolved trees.

Homoplasy.—Obviously, the degree of resolution of the particular cladogram examined will affect the level of homoplasy among taxa. Because the branch-and-bound analysis resulted in 13 equally parsimonious well-resolved trees and the comparison of all analyses suggest a minimally resolved polytomy within *Scalesia*, the level of homoplasy discussed is based on the branch-and-bound consensus tree, which is intermediate in resolution (Fig. 2). *Scalesia* itself is delimited by five synapomorphies and 11 homoplastic apomorphies (two among *Scalesia* species, five with external taxa, and four occurring both inside and outside *Scalesia*). Of the 15 species and 6 clades in *Scalesia*, only 9 are delimited by unique apomorphies. Of the 90 total character-states apomorphic for clades and species, 14 (16%) are unique, 42 (46%) are homoplastic only within *Scalesia*, 9 (10%) are homoplastic only between *Scalesia* and external taxa, and 25 (28%) are homoplastic between *Scalesia* taxa as well as with external taxa. It will be of interest to see the level of morphological homoplasy on DNA-sequence trees when these become available.

TABLE 3. Characterization of habitats of *Scalesia* species, estimated from the literature.

	Moist Forest Zone	Littoral Zone	Arid Zone	Dry Forest Zone	Volcanic Soil	Lava Gravel	Fissured Lava
<i>cordata</i>	x				x		
<i>microcephala</i>	x				x	x	
<i>pedunculata</i>	x				x	x	
<i>affinis</i>	x	x	x	x	x	x	x
<i>villosa</i>		x	x			x	x
<i>atractyloides</i>		x	x			?	x
<i>stewartii</i>		x	x			x	x
<i>incisa</i>		?	x			x	
<i>baurii</i>	?		x	x	?	x	
<i>retroflexa</i>		x				x	x
<i>helleri</i>		x	x			x	x
<i>gordilloi</i>		x	x	x		x	
<i>divisa</i>			x	x		x	x
<i>aspera</i>		x	x	x		x	x
<i>crockeri</i>		x				x	x

The characters that (at least some states of which) are not homoplastic in *Scalesia* include tree habit, leaf outline, leaf marginal lobing, dense villous hairs on abaxial leaf and phyllary surfaces, petiole shape, phyllary shape, ray orientation, palea segment shape and orientation, disk corolla color, disk corolla shape, anther appendage color, achene pubescence, and pappus development. However, all other characters and some states of the above are homoplastic. Some interesting examples include: 1) the presence of villous hairs in *S. villosa* and *Pappobolus*; 2) more or less solitary capitula of most species of *Scalesia* and *Viguiera grammatoglossa* and *V. stenoloba*; 3) multiple changes in size of capitula in *Scalesia*; 4) phyllary shape in *S. crockeri* and *Helianthus*; 5) palea length in *S. microcephala*, the elongate bracted clade, and *Pappobolus*; 6) glabrous paleae in *S. aspera*, *S. baurii*, *S. incisa*, *S. microcephala*, and *Pappobolus*; 7) length of the central lobe of the paleae in *S. affinis*, *S. crockeri*, *S. microcephala*, *S. villosa*; 8) disk corolla tube length in *S. affinis*, *S. baurii*, *S. stewartii*, the lobe-leaved clade, and *Viguiera adenophylla*; and 9) glabrous disk corolla tubes in *S. affinis*, *S. aspera*, *S. villosa*, the arboreous clade, and *Simsia*. Many of these characters are associated with the palea and corolla structure. According to Plovanich and Panero (2004), such characters associated with reproductive success should be convergent in the Heliantheae due to strong selection pressures. Whether this will be true in *Scalesia* remains to be investigated using molecular data sets.

In regard to the presence of rays in certain species of *Scalesia*, Eliasson (1974) concluded that rays were lost in the ancestor of *Scalesia*, regained as scattered bilabiate disk corollas in the lobed-leaved species, and regained as nearly typical rays in *S. affinis*. His hypothesis is supported by the results presented here. If the *affinis*-type rays are the end of a character transformation involving the bilabiate disk corollas or are a reversal to true rays, then this constitutes an additional homoplastic trait. Presumably rays increase insect pollination and should be selected for on islands as the insect fauna diversifies, as suggested by the wider distribution of *S. affinis*. However, the addition of artificial rays to *S. pedunculata* did not increase its fitness (Nielsen et al. 2002). Therefore it is not clear that this character has high adaptive value in *Scalesia*.

Despite the species and clades of *Scalesia* being delimited primarily by unique combinations of homoplastic character states as opposed to unique apomorphies, the species all appear to be distinct. Moreover, the full data set suggests that there is a real lack of morphological synapomorphy/autapomorphy within the continental genera because many species groups and species are likewise defined only by unique combinations of homoplastic characters states, not unique states.

Distribution in relation to phylogenetic results and homoplasy.—Because the oldest islands in the archipelago are in the southeast and the youngest in the west and northwest, correlation of geology with the cla-

dograms is not straightforward. If the species diverged from east to west, the basal split should produce a group of eastern species with the western species the most derived. However, the main split is between lowland and upland species. This may suggest that the lowland species diverged after the older islands from San Cristóbal west to Santiago were already in place and the lineage ancestors were able to disperse among islands easily. Among the upland species, *Scalesia microcephala* and *S. cordata* (basal in some results) occur on the youngest islands. Presumably, *Scalesia pedunculata* was already distinct and dispersed on the older islands and founded populations on the new volcanoes that later formed Isabela to originate the two other arboreal species.

Species of *Scalesia* are characterized by nearly allopatric distributions in similar habitats (12 spp. in arid communities, 3 spp. in upland moist communities) within the archipelago. The only synapomorphy correlated with the origin of the upland-habitat lineage is the tree growth habit, though four homoplastic characters also accompany the habitat (loss of leaf adaxial strigosity, moderately sized capitula, glabrous paleae, and corolla tube glabrous). The development of arborescence in a moist habitat under reduced competition is easy to understand (see Itow 1995; Hamann 2001), but further study is needed to determine if the other apomorphies are correlated with reproductive ecology. Eight homoplastic apomorphies but no synapomorphies are correlated with origin of the lineage in the lowland habitat (pubescence strongly strigose, elliptic leaves with entire margins, solitary capitula, blunt phyllaries, paleae deeply divided into elliptic lobes, achenes lacking awns). Unless additional environmental factors, such as humidity, ion content, pollinators, or dispersers, etc. significantly differentiate among both lowland and upland habitats, the species within these two elevational zones appear to occupy nearly the same range of habitats. For example, *Scalesia villosa* is the only *Scalesia* species having a dense covering of villous hairs, which presumably functions as a protection from high solar radiation. But several species occupying such habitats are not villous even though villous hairs occur in the related genera. Although *S. helleri* bears pinnatifid leaves as an autapomorphy, the nearly parapatric and perhaps sister species is distinguished only by two homoplastic apomorphies. Only a single autapomorphy (fully winged petioles) and three homoplastic traits distinguish *S. crockeri*; nearly parapatric with it is *S. aspera*, which is differentiated by only four homoplastic traits. Furthermore, diversification among the lowland species has resulted in some sharing apomorphies with some or all of the upland species and vice versa. *Scalesia microcephala* of mesic forests shares two palea character states (see above) with *S. villosa* but not with its close congeners in the mesic zone. Thus, demonstrating adaptation of distinguishing features of these species may prove to be challenging.

Speciation Patterns.—Because the sister-group to *Scalesia* remains obscure, comparison of speciation amounts among clades is not possible. It is apparent that this situation will not change until multiple congruent lines of molecular evidence resolve the relationships of the infrageneric groups of *Viguiera* and other genera in the derived Helianthinae. However, if a DNA sequence in which there is variation among species of *Scalesia* can be found and analyzed, then, at least speciation rates within *Scalesia* should be forthcoming.

Sampling recommendations.—Given the above situation, it is clear that sampling for future phylogenetic analyses should include, in addition to the present taxa, at least species of *Tithonia*; *Viguiera* subg. *Amphilepis*, sect. *Maculatae*, and sect. *Paradosa*; and other segregate genera of the derived Helianthinae. When congruent lines of molecular evidence point to one of these lineages as sister to *Scalesia*, a complete sampling of species should be attempted to determine whether the whole lineage or a subset of species is the actual sister to *Scalesia*.

CONCLUSION

The present study provides a large morphological data set for comparison with molecular phylogenies of *Scalesia* and close relatives when the molecular data become available. The results confirm that additional taxa and DNA sequences must be sampled to resolve the intergeneric and internal relationships of *Scalesia*. Furthermore, divergence of *Scalesia* from its origin to terminal speciations is characterized by combinations of homoplastic apomorphies. Likewise divergence and inter-island geography appear to be poorly correlated. The seeming uniformity within habitat zones, though, appears to be correlated with the homoplasy associated with divergence in *Scalesia*. Determining the degree to which these homoplastic morphological apomorphies are adaptive should clarify the process of speciation in this and other island endemics.

[illegible]

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